

Some Genetic Studies of Müllerian Mimics in Butterflies of the Genus *Heliconius*^{1, 2}

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(Plates I & II)

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[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I." by William Beebe, Zoologica, 1952, Vol. 37, No. 13, pp. 157-184].

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I. INTRODUCTION

THE genetic study of Batesian mimicry is quite well advanced, particularly in the genus *Papilio*. The data so far amassed suggest that the evolution of this type of mimicry is initiated by the presence of a phenotype with an imperfect resemblance to the model, as a result of mutation. If the new mutant is established by selection, modifiers of it are accumulated, which improve the resemblance of the mimic to the model (Clarke & Sheppard, 1962). The genetic investigations have been facilitated by the widespread occurrence of polymorphism

in Batesian mimics. Such polymorphisms would be expected on theoretical grounds, but in Müllerian mimicry they should not occur since the evolution of this type of mimicry should lead to monomorphism (Carpenter & Ford, 1933). Nevertheless, many Müllerian mimics, particularly in the genus *Heliconius*, are polymorphic. A previous study (Turner & Crane, 1962), together with the present one, were started to gather data on the mode of inheritance of some of these polymorphic forms—data essential to any subsequent work on the evolution of Müllerian mimicry in general and the maintenance of polymorphisms in such mimetic species in particular.

II. MATERIALS AND METHODS

The species investigated genetically are the South American butterflies *Heliconius numata*, *Heliconius doris*, *Heliconius melpomene* and *Heliconius erato*.

The technique of hand-mating butterflies (see Clarke & Sheppard, 1956) has proved extremely useful in genetic investigations of Batesian mimicry, since it has often allowed one to obtain species hybrids which could not otherwise have been produced. It has the further advantage of eliminating the necessity of having large mating cages. Since the study of Müllerian mimicry will often require the production of species hybrids, attempts were made to hand-mate members of the Heliconiinae. It was found that *Dione juno*, which will not readily pair in insectaries or lay eggs in them, could be hand-paired without much difficulty. The mated females would lay eggs in black silk organza sleeves placed over their food plant, *Passiflora serrato-digitata*. However, since the butterfly is not polymorphic, no further work was done with it. It was also found

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that *H. numata* and *H. erato* could be hand-paired and *H. erato* could be induced to lay eggs in silk organza sleeves. However, since the species proved refractory with respect to both the techniques, these methods were abandoned. Only one mating reported here, that between two *H. numata*, was obtained by hand-mating. All the broods of *H. melpomene* and *H. erato* were bred by the methods described by Turner & Crane (1962). The insects were placed in large insectaries and the females were allowed to lay eggs on cut food plant in their cages. The eggs were collected every evening and each egg was placed in a separate labelled dish and from then on each individual was kept isolated from all others.

H. doris has not yet been mated successfully in insectaries, since it requires a very tall cage to fly in. Nor would it lay eggs in the cages available or in silk organza bags, although one female did lay two eggs in such a bag. It is fortunate, therefore, that the species does not lay eggs singly, but deposits them in large rafts, of fifty to one hundred and fifty eggs (Beebe, Crane & Fleming, 1960). Consequently, to investigate the genetics of *H. doris*, egg rafts were collected in the wild and the resulting larvae were reared on cut food plant in jars of water in the laboratory.

Origin of Breeding Material and Description of Forms

The specimens of *H. numata* used in this study were taken from a colony living by the sides of Andrew's Trace, ten miles from Arima near the pass on the Arima-Blanchisseuse Road, Trinidad. A small random sample of adult butterflies was collected by netting them as they flew across the Trace running through the colony. The pair of insects used for the hand-mating and breeding came, however, from a stock raised in the insectaries. This stock originated from eggs and larvae collected off the food plant of the species on Andrew's Trace.

There are two forms of *H. numata* in Trinidad, a brown one which has yellow near the apex of the forewing, but none on the hindwing, and a yellow form which has an increased amount of yellow on the forewing and a yellow stripe on the hindwing which replaces a brown one of the other form (Plate I). There are a number of other minor differences of pattern with which we need not concern ourselves here.

The *H. doris* broods reported in this paper were all collected as egg rafts in the wild in Trinidad, except Brood 5 which was taken as a tight group of 2nd instar larvae. Broods 1 and 2 were found on the Texaco oil field near Guaya-

guayare, and Broods 3, 4 and 5 were found near Arima. In the case of Brood 4, the female was actually seen to be laying eggs when the egg raft was first discovered.

There are three main forms of *H. doris* in Trinidad, but the commonest form appears to be the "blue" one, *doris*. This has the usual black forewing with the two yellow patches on it (Plate I) and a black hindwing with a blue basal area from which short blue rays extend into the black area. The second form is the "red" one, *delila*. This is like the blue form except that there is no blue but in contrast there is a red area at the base of the forewings and the hindwings. From the basal red area on the hindwings, red rays extend out towards the margin of the wings. These rays are far longer than the blue ones of the "blue" form. The third form is the "green" one, *viridis*, and it is much like the blue phenotype except that the blue is replaced by green or blue-green.

The *H. melpomene* were obtained from two sources, Trinidad and Surinam. The Trinidad material was obtained as live adult butterflies caught near Arima. The Surinam insects came from Moengo. They were obtained as eggs, larvae, or adult butterflies from the vicinity of the old mine, the new mine and the wharf at Moengo itself.

In Trinidad the species is monomorphic for the broad-banded form which has black fore- and hindwings with a broad red band near the apex of the forewings (Plate II). In Surinam the species is highly polymorphic and among the many forms there are six main types, five of which are described and figured by Turner & Crane (1962). Besides the broad-banded Trinidad form, there is an extremely similar form but with a narrow band on the forewings instead of a broad one (narrow banded). The third form, broad-banded dennis, is similar to the broad-banded form except that there is an extra red area at the base of the fore- and hindwings. The fourth form, narrow-banded dennis, is similar to dennis except that it has a narrow band near the apex of the forewing instead of the normal broad one. The fifth form, broad-banded radiate, is like broad-banded dennis but in addition has red ray-like marks extending from the basal red area of the hindwings and the sixth form, narrow-banded radiate, is similar to broad-banded radiate except that it has a narrow band near the apex of the forewing. Thus the six forms consist of three main patterns, banded, dennis and radiate, in each of which the band common to all can be either broad or narrow (Plates I & II).

The *H. erato* were obtained in the same places and the same manner as were *H. melpomene*. In Trinidad *H. erato* is monomorphic; the form

found there, the broad-banded form, is so close in appearance to the local *H. melpomene* that only an expert investigator can tell them apart. In Surinam there are forms which parallel those of *H. melpomene*. Besides the broad-banded form there is a second which in some ways resembles narrow-banded in *H. melpomene* and in consequence we have called it narrow-banded. However, although the amount of red appears to be reduced in this form, this is achieved by an invasion of black pigment into the red bar rather than by a distinct narrowing of the bar itself. There are two other forms equivalent to dennis with broad bands and dennis with "narrow bands," but we have not, as yet, found these in the wild. In *H. erato*, dennis differs from the similar form in *H. melpomene* in that there is no red basal area on the hindwing. The fifth form is broad-banded radiate which has the *H. erato* broad-banded dennis pattern with the addition of rays on the hindwing. These rays are longer and of a different shape from those in the equivalent form in *H. melpomene*. The sixth form is like broad-banded radiate, but has narrow bands of the *erato* shape (Plates I & II).

III. RESULTS

H. numata

In Table I are given the results of hand-mating a virgin female *H. numata* with a male of the same species, both being of the yellow form. Not only the yellow but also the brown form of the species appeared among the offspring, showing that brown is recessive. There is no evidence of sex-linkage but the ratio of yellow to brown departs significantly from the 3:1 ratio expected on the simple hypothesis that the two forms are controlled by a pair of autosomal allelomorphs ($\chi^2_1=11.11$ $p<0.01$). The proportions do not differ significantly from the 2:1 ratio expected if the homozygous yellow individuals are lethal ($\chi^2_1=3.37$). This hypothesis cannot be accepted as it stands, however, because homozygous yellow individuals almost certainly exist in nature. In one of the insectaries a number of yellow wild *H. numata* females were allowed to lay eggs. Over a period of days they produced 15 yellow offspring and no brown ones, which is a

significant excess of yellow over the expected 2:1 ratio if all yellow females were heterozygous and were mated with heterozygous yellow males, let alone the ratio expected if some of the males had been homozygous browns. Since the two yellow parents in the brood came from the insectary, they may have been the offspring of the same parents. If this be so and if one of the parents had been carrying a lethal gene closely linked to the allelomorph controlling yellow, a 2:1 ratio would not be unlikely.

There is a second hypothesis which must also be considered. The observed ratio is very close to the 9:7 ratio expected from a modification of the 9:3:3:1 ratio due to epistasis where brown is recessive and controlled at two independent loci. Only more genetic work could distinguish between the hypothesis of a lethal and that of two independent loci with epistasis.

Before the breeding results had been obtained, it was decided to take a random sample from the wild population at Andrew's Trace in order to estimate the gene frequencies. The sample is given in Table II. Although gene frequencies cannot now be estimated, the data suggest that the frequency of brown may be increasing in Trinidad. Kaye (1921) reported that the brown

TABLE II. RANDOM SAMPLE OF *H. numata* FROM ANDREW'S TRACE, ARIMA VALLEY, TRINIDAD, TAKEN BETWEEN 16 AUG. AND 17 SEPT. 1962

Form	Male	Female	Total
Yellow	24	10	34
Brown	6	5	11

form was very rare in Trinidad in the past. He said "Until recent years the dark forms without yellow in the hind wing and with reduction of yellow in the fore wing were only rarely met with and in fact I never saw such absolutely typical *numata* from Trinidad until this year." It is true that the population referred to by Kaye is some fourteen miles from Andrew's Trace, but it is situated on the same range of mountains and the insect is a powerful flier, so that the two populations are not likely to be very effectively isolated.

TABLE I. BREEDING DATA FOR *H. numata*

Form of Parents		Form of Offspring				Total
Male	Female	Male		Female		
		Yellow	Brown	Yellow	Brown	
Yellow	Yellow	11	15	15	7	48

TABLE III. BREEDING DATA FROM *H. doris*. BROODS COLLECTED AS EGG RAFTS IN THE WILD IN TRINIDAD, SEPT. 1962

Brood	Form		
	Blue	Red	Green
1	68	—	—
2	Male 11	Male 6	—
	Female 14	Female 10	—
3	40	—	—
4	12	—	10*
5	Male 53	Male 57	Male 1
	Female 33	Female 26	Female —

*One was intermediate.

H. doris

The broods resulting from egg rafts of *H. doris* found in the wild in Trinidad are given in Table III. Two of the broods did not segregate, giving only the blue form. Nos. 2 and 5 segregated for the red form, and No. 4 for the blue and green forms with one intermediate.

The clear-cut segregation in Broods 2 and 5 indicates that red is inherited on a simple Mendelian basis. The ratio in Brood 2 suggests a difference from a ratio of three blue to one red ($p \approx 0.05$), expected if red is recessive (see below) and it is far closer to a 1:1 ratio ($\chi = 1.98$). Brood 5 shows a very close approach to a 1:1 ratio of red to non-red, and is different from a 3:1 ratio ($p < 0.001$). The single green individual may be genetically blue since it is not very extreme (but see below).

H. doris tends to fly rather high and very fast and is therefore difficult to catch. It has not been easy to obtain a random sample to determine the frequency of the various morphs. However, a number of these insects were caught in both Trinidad and Surinam. To augment the sample, a record was kept of all other specimens which were seen but not caught (Table IV). It is realized that such a procedure may allow an individual butterfly to be counted more than once, but with such a powerful flier, not many individuals are likely to be so counted.

The data, such as they are, indicate that the

frequency of the red form is low, and that the green form is even rarer in Trinidad. The data indicate, but do not prove, that the red form is somewhat commoner in Surinam. However, the segregation of red in 2 out of 5 broods indicates a higher frequency than that found for red in the random sample from Trinidad. If the frequency of the red form is low, then the most likely mating to produce a segregating brood is between two heterozygotes (giving a 3:1 ratio) if red is recessive, but a back-cross (giving a 1:1 ratio) if red is dominant. It seems probable that both segregating broods are giving a 1:1 ratio and that it is likely therefore that red is dominant to blue, although more data are required to substantiate this point.³

The brood segregating only for the blue and green forms also appears to be a back-cross (although not significantly different from a 3:1 ratio), and since green is even rarer than red in Trinidad, it seems likely that green is also dominant to blue. In neither segregating brood can egg rafts of mixed parentage explain the approach to a 1:1 ratio. Both the red and green forms appear to be rarer than blue in Trinidad and consequently if two or more females had

³Three additional broods were obtained in Sept., 1963, and produced the following phenotypes: No. 6, 16 red ♂, 13 red ♀; No. 7, 19 red ♂, 18 red ♀, 7 blue ♂, 9 blue ♀, 8 green ♀; No. 8, 11 red ♂, 6 red ♀, 2 blue ♂, 1 blue ♀. No. 8 departs significantly from a 1:1 ratio ($p < 0.01$) and agrees well with a 3:1 ratio, confirming that red is dominant.

TABLE IV. RECORD OF THE NUMBERS OF EACH FORM OF *H. doris* SEEN OR CAUGHT IN SURINAM JULY 21 TO AUG. 3, 1962, AND IN TRINIDAD, SEPT. 1962

	Forms					
	Blue		Red		Green	
	Caught	Seen	Caught	Seen	Caught	Seen
Surinam	4	8	2	1	0	0
Trinidad	8	7	1	0	0	0

laid the batch, the number of the rarer forms would be reduced, not augmented to give an approximation to a 1:1 ratio. Moreover, in Brood 2, the distribution of the eggs and way they hatched indicated that the batch was not laid by more than one female, and Brood 5 also appeared to be a homogeneous group.

The single green individual in Brood 5 might be thought to indicate a mixed brood, since its presence cannot be explained on any simple Mendelian basis. However, the similar size of the larvae and the emergence date of the adults gave no evidence of heterogeneity. It seems more likely that it is a phenocopy, since it is not very extreme. It could however be explained as being due to a cross-over, if there are 2 closely linked genes concerned and red is epistatic to green, the red parent being a double heterozygote with the genes in coupling.⁴

H. melpomene

Turner & Crane (1962) showed that in *H. melpomene* the dennis pattern is dominant to the broad-banded form and is controlled by an autosomal locus. The radiate pattern is also controlled by a single gene, but since the only brood they produced was a back-cross, they could not be certain of the dominance relationships. However, they suggested that it was probably dominant. Since the radiate pattern incorporates the dennis pattern in their brood and rays on the hindwings are never found without the dennis pattern in Surinam, although they are elsewhere, they assume that the dennis pattern and the presence of rays on the hindwing are controlled by two very closely linked genes. However, they also mention the possibility that the gene producing rays is at an independent locus, but can only produce its effect in the presence of the dennis pattern. They also showed that their narrow-banded pattern was controlled by a locus closely linked to that producing dennis, and moreover that narrow-bandedness was recessive.

The present investigation was undertaken to extend their work, in particular to measure the cross-over value between the loci controlling dennis and narrow bands. Our results (Table V) confirm that dennis is not recessive, since it produced a good 1:1 ratio in back-crosses, including those to the monomorphic Trinidad race. The data also showed that radiate is not sex-linked and is not recessive since it appeared in a 1:1 ratio in crosses with the monomorphic race, but since we produced no homozygotes, I do not

know if it is a complete dominant. It was possible to show that rays on the hindwing are not controlled by an independent locus, which only produces its effect in the presence of the dennis pattern, since the dennis pattern and the presence or absence of rays did not segregate independently in the back-cross to the Trinidad broad-banded form (Broods K.18, K.21, K.22, K.23). It might be argued that the Trinidad race is homozygous for the gene producing rayed hindwings, but that it produces no effect because dennis is not found in that race. However, a male that produced a 1:1 ratio of radiate to non-radiate individuals when mated to a radiate female, produced a brood which segregated in a 1:1 ratio for dennis and non-dennis, when mated to a dennis individual (Broods K.23, K.24). Thus it is clear that the male was not carrying an allelomorph, at an independent locus, producing rayed hindwings only in the presence of dennis. In those back-cross broods appropriate for showing crossing-over between dennis and rays, there is no certain indication that the dennis pattern and rays are separated by crossing-over. It is true that the dennis pattern did appear in such a brood (K.22) but I attribute this to a mistake rather than a cross-over, since no individuals without dennis but with rays on the hindwings (the other cross-over class) appeared. Thus the data support that of Turner & Crane (1962) in suggesting that the dennis and ray patterns are controlled by two very closely linked genes, or perhaps by allelomorphs at one locus.

Narrow Bands

A number of narrow-banded forms, indistinguishable morphologically from those described by Turner & Crane, were obtained from Moengo where they had obtained their butterflies. However, the narrow-banded form I obtained is not recessive, since it produced such forms in the cross with the monomorphic Trinidad race. Moreover, broad-banded forms were obtained among the progeny of parents, both of which were narrow-banded (Broods C.3, C.11). These broods also produced insects which had much more yellow on the forewings than is usual in narrow-banded forms. If such broods are divided into broad-banded forms, narrow-banded ones and narrow-banded ones with an excess of yellow, a good approach to a 1:2:1 ratio is obtained ($\chi^2_2 = 2.28$ $p > 0.3$), indicating that narrow bands are incompletely dominant (Table VI). One of these yellow individuals proved to be a homozygote on back-crossing to a heterozygote, and its offspring segregated out in a 1:1 ratio for narrow-band and narrow-band with excess yellow (Table VI). A few undoubted narrow-banded

⁴Brood No. 7 supports the hypothesis that red is either dominant or epistatic to green. The sex ratios of the blue and of the green forms are not significantly different ($p > 0.05$).

TABLE V. BREEDING DATA FROM *H. melpomene*

Brood	Parents and Origin		Phenotype of Offspring										Total		
			BR		BD		B		NR		ND			N	
	Female	Male	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		♂	♀
C.1	T.B.	S.N	0	1	0	0	6	7	0	0	0	0	2	2	18
C.3	S.N.	S.N ¹	0	0	0	0	1	2	0	0	0	0	3	3	9
C.4	S.BD	S.N ¹	0	0	1	0	0	0	0	0	0	0	0	0	1
C.4b	C ₁ .N	S.BR	3	2	0	0	4	5	1	3	0	0	4	1	23
C.7	S.BD	S.N ¹	0	0	1	4	1	6	0	0	3	1	1	3	20
C.8	S.BR	S.N ²	13	23	0	0	14	16	10	26	0	0	15	23	140
C.9	S.BD	S.N ²	0	0	2	6	3	2	0	0	10	8	9	8	48
C.10	S.N	S.N ²	0	0	0	0	0	0	0	0	0	0	4	3	7
C.11	S.N	S.N ²	0	0	1	0	5	5	0	0	0	1	7	6	25
C.12	S.BD	S.N ³	0	0	3	1	2	0	0	0	1	2	3	1	13
C.13	S.ND	T.B	0	1	1	0	4	3	0	0	3	4	5	4	25
C.14	S.B	S.BR	0	1	0	0	0	0	0	0	0	0	0	0	1
C.17	S.BD	S.N ¹	0	0	0	0	0	1	0	0	1	0	0	0	2
K.4	C ₃ .N	C12.N	0	0	0	0	0	0	0	0	0	0	27	23	50
K.6	C8.BR	S.N ³	17	13	0	0	13	10	14	16	0	0	4	11	98
K.10	C13.ND	T.B	0	0	1	4	2	4	0	0	1	2	2	2	18
K.11	C7.ND	C8.B	0	1	3	4	12	5	0	0	7	10	2	3	47
K.12	C9.B	C7.ND	0	0	8	9	7	9	0	0	13	15	8	11	80
K.14	C7.BD	S.N ²	0	0	7	12	8	14	0	0	13	13	13	11	91
K.17	C8.NR	C7.B	3	3	0	0	1	3	0	2	0	0	2	0	14
K.18	C8.NR	T.B ⁴	2	3	0	0	5	2	5	4	0	0	2	4	27
K.20	C8.NR	C11.B	3	3	0	0	4	6	4	3	0	0	3	3	29
K.21	C8.BR	T.B ⁴	9	6	0	0	3	6	0	0	0	0	0	1	25
K.22	C8.NR	T.B ⁵	10	7	0	1	6	10	9	7	0	0	13	6	69
K.23	K.6.BR	T.B ⁵	6	4	0	0	8	18	0	0	0	0	0	2	38
K.24	K.14.BD	T.B ⁵	0	0	11	12	16	15	0	0	0	0	0	1	55

In the Table, S and T indicate the origin of the parents as Surinam and Trinidad respectively. Elsewhere the origin of the parent is indicated by its Brood number. The letters BR, BD, B, NR, ND and N stand respectively for the phenotypes broad-banded radiate, broad-banded dennis, broad-banded (the Trinidad phenotype), narrow-banded radiate, narrow-banded dennis and narrow-banded.

When a male has been used in more than one mating, it is distinguished by a superscript; thus the male parent of Broods K.22, K.23 and K.24 was the Trinidad broad-banded male No. 5.

There are clearly a few insects which have been included in the wrong broods by mistake—an almost unavoidable occurrence when breeding such large numbers of insects. These are indicated by being placed in italics.

heterozygotes in other broods have as much yellow on them as do some of the least extreme of the presumed homozygotes. Thus it seem likely that the heterozygotes and the homozygotes cannot always be distinguished.

That the narrow-banded forms in the broods reported here are different from the similar forms investigated by Turner & Crane is demonstrated by the linkage data as well as by the difference in the dominance relationships discussed above. The locus determining the narrow-banded form investigated by Turner & Crane was linked to that controlling the dennis pattern, whereas the present data give no indication of linkage between narrow-bands and either the dennis or the radiate patterns. Thus there are clearly two independent loci, both of which have allelomorphs producing a narrow-banded form.

H. erato

Turner & Crane demonstrated from Beebe's

(1955) data that the radiate pattern in *H. erato* is dominant to the non-radiate form and that the dennis and rayed components of the patterns are inherited together. The present data (Table VII) are in complete accord with this interpretation. Turner & Crane also showed that the narrow-banded form (which differs from that in *H. melpomene*, since the apparent reduction in red is achieved by an invasion of black pigment and not by a narrowing of the bar itself) is dominant to the broad-banded form. They also suggested that the locus concerned is linked to that controlling the radiate pattern. Our data confirm the dominance of "narrow-bands", since a 1:1: ratio was obtained in the back-cross to the monomorphic Trinidad race. However, in the brood in question (E.C.2) there is no evidence of linkage. Since the previous evidence for linkage was not statistically significant, there is no reason to postulate its presence on the evidence from the breed-

TABLE VI. BREEDING DATA FROM NARROW-BANDED
H. melpomene

	Parents form and origin		Phenotype of Offspring						Total
			B		N		NY		
	Female	Male	Male	Female	Male	Female	Male	Female	
C.3	S.N	S.N	1	2	1	1	2	2	9
C.10	S.N	S.N ²	0	0	2	3	2	0	7
*C.11	S.N	S.N ²	5	5	6	2	1	4	23
Total			13		15		11		39
K.4	C.3.NY	C.12.N	0	0	18	8	9	15	50

NY signifies that the narrow-banded form had more than the usual amount of yellow in the vicinity of the red narrow band. *The broad-banded and the narrow-banded dennis individuals have been excluded since their presence is clearly due to a mistake (in Table V).

TABLE VII. BREEDING DATA FROM *H. erato*

Brood	Parents and origin		Phenotype of Offspring								Total
			BR		B		NR		N		
	Female	Male	Male	Female	Male	Female	Male	Female	Male	Female	
EC.2	S.NR	T.B	2	3	4	3	1	3	1	4	21
EK.14	EC2.NR	T.B	0	0	1	0	0	0	0	0	1
EC.1	S.BR	S.?	1	0	0	1	0	0	0	0	2
EC.8	S.B	S.BR	2	1	0	1	0	0	0	0	4
EC.9	S.BR	T.B	3	1	3	5	0	0	0	0	12

TABLE VIII. PHENOTYPES IN RANDOM SAMPLES OF *H. melpomene* AND *H. erato* TAKEN AS ADULTS (A) AND AS EGGS AND LARVAE (E & L)

Species	Stage	Sex	Phenotypes						Total
			BR	BD	B	NR	ND	N	
<i>H. melpomene</i>	A	Male	0	0	12	0	0	2	21
		Female	1	0	6	0	0	0	
	E & L	Male	4	5	43	0	0	7	127
		Female	2	6	53	0	1	6	
Total			7	11	114	0	1	15	148
<i>H. erato</i>	A	Male and Female	5	0	40	4	0	6	55
	E & L	Male	3	0	5	0	0	1	18
		Female	2	0	4	2	0	1	
Total			10	0	49	6	0	8	73

ing data, nor to doubt that the same allelomorph was used in the two investigations.

Random Samples of H. melpomene and H. erato from Surinam

The forms found in *H. melpomene* and *H. erato* at Moengo in Surinam between July 21 and August 3, 1962, are given in Table VIII.

Each sample is divided into two groups consisting of those insects taken as adult butterflies and those found as either eggs or larvae. The two do not differ significantly from one another although there is a suggestion that there are more radiate forms among the egg and larval sample in *H. erato* than among the adults. This can hardly be due to non-random sampling of adults

since it is precisely the rare conspicuous radiate forms that the collector would tend to net if his collecting were not random. Of course, during the sampling every effort was made to keep the sample random.

From the random samples, estimates of the gene frequency can be made. For this purpose it has been assumed that in *H. melpomene* the forms non-dennis, dennis and radiate are controlled by three allelomorphs *d*, *D*, and *D^R* respectively and that all the narrow-banded forms are of the "dominant" type, controlled by a pair of allelomorphs *N^N* (narrow-banded) and *N^B* (broad-banded).

In *H. erato*, the allelomorph for the non-radiate pattern has been designated as *d*, and that for the radiate form as *D^R*. The allelomorph controlling the narrow-banded form is designated *B^b* following Turner & Crane and that for broad-banded *B*.

The gene frequencies estimated from the random samples are given in Table IX. No standard errors have been attached to these estimates since the method of sampling eggs and larvae might have resulted in an excess of offspring of some parents being included. However, the insects are powerful fliers and only lay between one and eight eggs a day, each being laid on a separate vine and not in quick succession. Thus there is little likelihood that the eggs and larvae sampled are not random with respect to the population in the locality.

IV. DISCUSSION

The very incomplete data on the inheritance of the morphs in *H. numata* and *H. doris* do not allow one to draw many conclusions on the factors responsible for the evolution and maintenance of the polymorphisms. However, if the red and green forms of *H. doris* are, in fact, dominant, then the mechanism maintaining the polymorphism is of acute interest, since at least the frequency of the gene controlling the green

form must be very low in Trinidad. Robertson (1962) has argued that under these circumstances, the polymorphism cannot be maintained by the advantage of heterozygotes in small populations. Furthermore he says "If the equilibrium gene frequency lies outside the range of 0.2 and 0.8 selection for the heterozygote may over a large range of population sizes in fact magnify the effect of reduced population size in leading to fixation." If Robertson is correct, it seems likely that the polymorphism for the green form in *H. doris* is maintained by some other mechanism than heterozygous advantage, since in Trinidad the population of this species is extremely sparse in some seasons. The elucidation of this mechanism, which can hardly be hybridization with other races since Trinidad is an island, would be of extreme importance to the theory of Müllerian mimicry.

The two species *H. melpomene* and *H. erato* show remarkable parallel variation with respect to their forms. But although the forms look much alike, they are morphologically different. Thus the apparent reduction of red in the narrow-banded form in *H. erato* is obtained by an invasion of black pigment into the red sub-apical band, whereas in *H. melpomene* it is by a narrowing of the band itself. The morphology of the rays in the radiate forms is also different in the two species, as is the distribution of red in the dennis pattern (Plate II).

The genetic control of the forms in the two species shows great similarities. In both species the radiate pattern is "dominant" and the dennis pattern and the rays are inherited together. Moreover, in both species there is a gene unlinked to that controlling the radiate pattern, which is dominant in effect and which reduces the amount of red on the forewing sub-apical bar. The recessive form of this phenotype, which is found in *H. melpomene*, has not yet been found in *E. erato*.

The more extensive data on the genetics of

TABLE IX. GENE FREQUENCIES ESTIMATED FROM RANDOM SAMPLES OF SURINAM *H. melpomene* AND *H. erato*

Species	Allelomorph	Frequency	No. in Sample
<i>H. melpomene</i>	<i>D^R</i>	0.024	148
	<i>D</i>	0.041	
	<i>d</i>	0.935	
	<i>N^N</i>	0.056	148
	<i>N^B</i>	0.944	
<i>H. erato</i>	<i>D^R</i>	0.116	73
	<i>d</i>	0.884	
	<i>B^b</i>	0.101	73
	<i>B</i>	0.899	

H. melpomene and *H. erato* show quite clearly that the genes controlling dominant characters in Surinam are at such low frequencies that the polymorphism falls into the category which Robertson believes cannot be maintained by an advantage of heterozygotes. The maintenance of the polymorphism in Surinam in fact may not be controlled by the action of selection in the area itself, but may be due to hybridization, since the frequency of the rarer forms appears to increase towards the east and decrease towards the west. If hybridization is important in this respect, it could explain another puzzling feature of the polymorphism. The heterozygotes for narrow band, dennis and radiate in *H. melpomene* and the narrow-banded and radiate forms in *H. erato* look very much the same in the F.1 Trinidad hybrids as they do in the pure Surinam stock. However, if there has been selection for an improved resemblance between parallel forms in the two species, owing to the mimicry, some breakdown in the pattern might have been expected (see Clarke & Sheppard, 1963). However, if the Surinam population is in reality itself a hybrid population, no such breakdown in the mimicry would be obtained. Only work on the genetics of populations to the east and to the south of Surinam can resolve these problems.

V. SUMMARY

1. The mode of inheritance of some of the polymorphic forms of the mimetic butterflies *Heliconius numata*, *H. doris*, *H. melpomene* and *H. erato* is described.

2. It was found that the Trinidad form of *H. numata* with yellow on the hindwings is dominant to that with no yellow. However, the exact mode of inheritance of the difference is not yet known, although certainly it depends on one or more major genes.

3. Data are presented which suggest, but do not prove, that in Trinidad the red and green forms of *H. doris* are dominant to the blue form.

4. It was confirmed that the "dennis" form of *H. melpomene* from Surinam, which has a red area at the base of the forewings and the hindwings, is dominant to "non-dennis." It was also shown that the radiate form from the same place, in which there are red rays on the hindwing in addition to the "dennis" pattern, is dominant or semi-dominant to its absence.

5. In previous work on the polymorphic Surinam population of *H. melpomene*, it had been shown that the form in which the red sub-apical forewing band is narrow (narrow-banded) is recessive to the broad-banded form (the only one in Trinidad) and controlled by a locus linked

to that determining the "dennis" pattern. In the present investigation, an independent locus was identified which controlled a second narrow-banded form. This new form is semi-dominant, the heterozygote being indistinguishable phenotypically from the recessive form.

6. It was confirmed from Surinam stock that the "radiate" pattern of *H. erato* is dominant to "non-radiate." Furthermore, the narrow-banded form of *H. erato*, in which black invades the red sub-apical band, is dominant to broad-banded, the only form in Trinidad. However, it is not linked to the locus controlling the "radiate" pattern as had previously been suggested.

7. The frequency of the allelomorphs controlling the dominant forms of *H. melpomene* and *H. erato* in Surinam suggests that the polymorphism may not be maintained by an advantage of the heterozygotes. It is suggested that the polymorphism results from hybridization between populations to the east and to the west of that country. It is pointed out that hybridization cannot explain the maintenance of the polymorphism in *H. doris* in Trinidad.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. *H. doris*, red form from Brood 2.
 FIG. 2. *H. doris*, blue form from Brood 2.
 FIG. 3. *H. numata*, brown form from Brood (Table I).
 FIG. 4. *H. numata*, yellow form from Brood (Table I).
 FIG. 5. *H. melpomene*, "dennis" form collected as a larva in Surinam.
 FIG. 6. *H. erato* collected as an egg from Surinam. This insect shows a tendency towards narrow bands, but it is phenotypically different, and may be genotypically different from the true narrow banded form of *H. erato* (see Plate II, Fig. 12).

PLATE II

- FIG. 7. *H. melpomene*, broad-banded form from Surinam.
 FIG. 8. *H. erato*, broad-banded form from Surinam. Note the close resemblance to the corresponding form in *H. melpomene* (Fig. 7).

- FIG. 9. *H. melpomene*, "radiate" form from Surinam. Compare the pattern with that of "dennis" (Plate I, Fig. 5), and "radiate" of *H. erato* (Plate II, Fig. 10).
 FIG. 10. *H. erato*, "radiate" form from Surinam. Note the difference between the rays in this insect and those in *H. melpomene* (Fig. 9).
 FIG. 11. *H. melpomene*, narrow-banded heterozygote from Surinam. Compare with the corresponding homozygotes (Fig. 7 and Fig. 13).
 FIG. 12. *H. erato*, narrow-banded from Brood EC.2. Note the difference between this form and narrow-banded in *H. melpomene* (Fig. 11).
 FIG. 13. *H. melpomene*, narrow-banded homozygote from Brood C.11. Note the difference between it and the heterozygous form (Fig. 11). The very pale areas are yellow and bordered towards the apex of the wing by a narrow red band. This band appears as a gray area in the photograph.

Except in Fig. 13, all the pale areas of the insects shown are red.